# Defense Strategies in Scale Insects: Phylogenetic Inference and Evolutionary Scenarios (Hemiptera, Coccoidea)

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### ABSTRACT

The sedentary plant-parasitic habit of scale insects increases their vulnerability to natural enemies and to adverse environmental factors. They have evolved a range of defense strategies which improve their chances of survival and reproductive success. These strategies are reviewed here. They include: 1. construction of protective structures from secretions and/or excretions produced by the scale insects; 2. behavioral adaptations to exploit host-plant afforded protection; 3. modifications of their life-cycle in response to environmental factors; and 4. modifications of the female body to provide protection for their progeny. The structure and formation of these protective structures were examined using SEM and by experimentation. A cladistic phylogenetic analysis of scale insects using 54 morphological characters and 25 genera resulted in two most parsimonious trees. This phylogeny was then used as a reference to provide hypotheses regarding the ancestral state and the subsequent evolution of habitat choice and the type of protective structure, especially in the nymphal stages. Phylogenetic analysis suggests that the ancestral habitat attribute (feeding site) is equivocal and currently we can not choose between the aerial (bark) or underground (roots) habitats. The subsequent adaptation led to colonization of branches, leaves and grasses. Most successful groups are adapted to the aerial part of woody host plants, particularly on the branches, which are the most exploited feeding sites by scale insect populations today. The ancestral type of protection is inferred to have been amorphous secretions. Subsequently, different clades probably independently developed protective tests with different combinations of secretions and anal fluid components, with a trend to find a compromise between energy costs and efficiency.

### RÉSUMÉ

**Stratégies de défense des Cochenilles : Inférence phylogénétique et scénarios évolutifs (Hémiptères : Coccoidea)**

La vie sédentaire des Cochenilles accroît leur vulnérabilité face à leurs ennemis naturels et aux conditions de l'environnement. Elles ont développé au cours de leur évolution diverses stratégies de défense, qui augmentent leurs chances de survie et leurs succès reproducteurs. Ces stratégies sont analysées, en distinguant parmi elles : 1. l'élaboration de structures de protection à partir de leurs sécrétions et/ou de leurs excrétions ; 2. l'exploitation de l'effet protecteur offert par leurs plantes-hôtes ; 3. la modification de leur cycle évolutif en réponse aux facteurs environnementaux ; 4. la modification profonde du corps des femelles pour la protection de leur descendance. L'utilisation du microscope électronique à balayage, ainsi que diverses expérimentations, ont permis d'expliquer la formation de ces structures. Une analyse cladistique portant sur 25 genres à partir de 54 caractères morphologiques a donné deux arbres équiparcimonieux. Cette phylogénie sert de référence pour établir l'état ancestral et les changements subséquents, à la fois pour le choix de l'habitat et pour le type de structure de protection. L'analyse phylogénétique suggère que l'état ancestral est équivoque et actuellement nous ne pouvons pas choisir entre un habitat aérien (tronc) et un habitat souterrain (racines). Il est plus parcimonieux de considérer la protection par des sécrétions amorphes comme l'état ancestral. Les changements subséquents de l'habitat ont conduit à la conquête des branches,

des feuillage des arbres et arbustes et des tiges de graminées. La branche est la partie la plus exploitée des plantes-hôtes. La protection a été tout d'abord assurée par des sécrétions non organisées recouvrant le corps, puis par la construction de structures de plus en plus complexes, avec une tendance à trouver un compromis entre les dépenses énergétiques et l'efficacité.

## INTRODUCTION

The adult females of contemporary scale insects are neotenic and apterous and are adapted to a sedentary parasitic habit, sucking sap from their host plant's vascular tissue. Not only have the Coccoidea colonized many plant families but they have also exploited all parts, with species living on the leaf sheaths, hypocotyl and roots of grasses and on the trunks, branches, leaves and fruits of shrubs and trees. Scale insects are often an important component of phytophagous ecosystems, especially in tropical and subtropical areas and many species are injurious to cultivated plants, such as vines, palms, citrus, forest or ornamental trees and also to indoor plants. They occur in all zoogeographical regions of the world and in a wide range of ecosystems, from dry desert to cold tundra, humid forest or high up mountains.

These sedentary insects have evolved a series of original and effective protective structures ensuring their survival in these diverse environments, providing not only a favorable microenvironment with regard to temperature and humidity, but also some degree of protection against such natural enemies as predators (mainly Coleoptera) and parasitoids (primarily chalcidoid wasps) and also against chemicals and air pollutants.

The scale insects are undoubtedly a natural group and their evolution is particularly interesting because the Coccoidea display a remarkable diversity of often unusual structural and biological features. However, the relationships of several family-group taxa, as well as the monophyly of some families remain controversial and not well established. Several authors have attempted to estimate phylogenetic relationships within the Coccoidea but until now such estimates have been largely intuitive. In these cases, the proposed phylogenies are not refutable and cannot be submitted to the test of adding new taxa and new characters. A comprehensive and interesting phylogenetic analysis of Coccoidea has been carried out by DANZIG (1980). The following works: DANZIG (1984, 1990), COX & WILLIAMS (1986), COX (1984), FOLDI (1984), KOTEJA (1974), BORATYNSKI & DAVIES (1971) and BORCHSENIUS (1956) used analytical methods other than cladistics and are, therefore, less easily supported. MILLER & KOSZTARAB (1979) and KOSZTARAB (1996) presented phylograms of the intuitively modified cladograms of BORATYNSKI & DAVIES (1971) and DANZIG (1980), respectively. The use of cladistic analysis has recently been developed among coccidologists to estimate sister-group relationships within the Coccoidea (MILLER, 1984; MILLER & MILLER, 1993a, 1993b; FOLDI, 1995; MILLER & WILLIAMS, 1995; QIN & GULLAN, 1995; HODGSON & HENDERSON, 1996).

In the present work, the adaptive defense strategies in scale insects were studied, and in order to test various scenarios for the evolution of the main habitats and protective structures for some of the main taxa of the Coccoidea, an independently reconstructed phylogeny was used as reference (CODDINGTON, 1988; CARPENTER, 1989; DELEPORTE, 1993; GRANDCOLAS *et al.*, 1994, DESUTTER-GRANDCOLAS, 1994; MILLER & WENZEL, 1995; ANDERSEN, 1995; SCHULTZ *et al.*, 1996). These biological attributes (habitat and type of protective cover) have been mapped on a cladogram and polarized by optimization with principle of parsimony and it is hoped that this may provide a reasonable hypothesis of the ancestral state and its subsequent direction of historical transition.

## MATERIALS AND METHODS

*Porphyrophora chrithmi* was reared in a greenhouse on *Crithmum maritimum* (Umbelliferae), whereas *Eurhizococcus brasiliensis, Margarodes cadeti, M. vitis* were reared on *Solanum tuberosum and Cucurbita maxima* and *Eriococcus buxi* on *Buxus sempervirens.* Cladistic analysis was implemented with the Paup 3.1.1. (SWOFFORD, 1991) and MacClade 3.05 (MADDISON & MADDISON, 1992) computer software packages. Character change analysis was performed by MacClade and the parsimony analysis of the character matrix with the "Heuristic search" algorithm of Paup with the "acctran" optimization. Multistate characters were treated as unordered and characters were unweighted. Unknown characters were coded as missing data. The size and structure of data matrix prevented the use of the exhaustive or branch and bound methods. The data matrix included 25 genera, representing each of the currently recognized scale insect families, with 54 characters from adult females, adult males and first-instar nymphs. Data were gathered either from published information (GREEN, 1922; JAKUBSKI, 1965; RICHARD, 1986; TAKAGI, 1987, 1992; GILL, 1988, 1993; KOSZTARAB & KOZAR, 1988; WILLIAMS & WATSON, 1990; MORALES, 1991; MILLER, 1991; MAROTTA *et al.*, 1995) or from direct examination of specimens as follows: *Matsucoccus feytaudi* Ducasse (Margarodidae); *Margarodes formicarum* Guilding (Margarodidae); *Stigmacoccus asper* Hempel (Margarodidae); *Carayonema orousseti* Richard (Carayonemidae); *Orthezia urticae* (Linnaeus) (Ortheziidae); *Phenacoleachia zealendica* (Maskell) (Phenacoleachiidae); *Conchaspis vayssierei* Mamet (Conchaspididae); *Planococcus citri* (Risso) (Pseudococcidae); *Eriococcus buxi* (Fonscolombe) (Eriococcidae); *Kermes vermilio* Planchon (Kermesidae); *Dactylopius coccus* Costa (Dactylopiidae); *Coccus hesperidum* Linnaeus (Coccidae); *Cerococcus quercus* Comstock (Cerococcidae); *Asterodiaspis variolosa* (Ratzeburg) (Asterolecaniidae); *Lecanodiaspis sardoa* Targioni-Tozzetti (Lecanodiaspididae); *Aclerda berlesii* Buffa (Aclerdidae); *Tachardia albizziae* Green (Tachardiidae); *Micrococcus silvestri* Leonardi (Micrococcidae); *Stictococcus intermedius* (Stictococcidae); *Phoenicococcus marlatti* Cockerell (Phoenicococcidae); *Halimococcus thebaicae* Hall (Halimococcidae); *Beesonia napiformis* Kuwana (Beesoniidae); *Chionaspis salicis* (Linnaeus) (Diaspididae). The aphids (Aphidoidea), traditionally considered as forming the sister-group of the Coccoidea and recently confirmed by cladistic analysis of molecular data (SORENSEN *et al.*, 1995; VON DOHLEN & MORAN, 1995), were used as outgroup to determine polarities of characters (*Eriosoma* spp. (Pemphigidae) and *Myzus persicae* (Aphididae).

To test hypotheses regarding the evolution of particular biological attributes, this independently obtained cladogram was used as a reference system. The biological attributes (habitats, *i.e.* feeding sites on host plants, and protective structures) were then mapped on this cladogram. The scenario for their evolutionary changes was derived by optimization using the principle of Wagner parsimony and unordered states with MacClade 3.05 computer software.

## TYPES OF DEFENSIVE STRATEGIES OF SCALE INSECTS

The strategies which have evolved to defend the bodies of scale insects and their progeny (eggs and newly hatched first-instar nymphs) can be divided into four major groups:

1. production of structures which are made from secretions and/or excretions which either adhere to the body or form amorphous waxy secretions, cysts or separate tests; this type of protection, from simple to complex, is the most widespread and the most characteristic of Coccoidea;

2. specific choice of settling site to exploit host-plant afforded protection (*e.g.* those which live beneath bark, under leaf-sheaths or on the nodes of grass stems, or which are gall formers);

3. modifications of the life-cycle in response to environmental factors, as found in the cyst-forming Margarodinae;

4. modification of the body of the female to provide a protective cover, such as by the formation of a marsupium, as in the Margarodids, or the heavy sclerotization of the dorsum of soft scales, in Kermesids or Stictococcines.

All Coccoidea are protected by one of the mechanisms described above. In some unrelated groups or in groups in which the protective mechanism has evolved convergently, it is probably dictated by habitat-required defense strategies. However, JASCHENKO (1993) observed that some Margarodids living in desert may utilize complementary protection and show particular ecological adaptations, *e.g.* the scale insects may form a buffer layer around their body or leave

the soil surface for a deeper ground layers. Mutualistic relationships with ants may appear in some group as an alternative strategy for their protection. These four categories will now be discussed in more detail.

## STRUCTURES CONSTRUCTED FROM SECRETIONS / EXCRETIONS PRODUCED BY SCALE INSECTS

Most scale insects secrete a series of external protective covers during each stage of their development. These covers or tests regulate the temperature and control water loss, thus maintaining an equable microclimate beneath the test, so that, when the test is removed, the Coccoids die through desiccation. The diverse methods which have evolved to protect the eggs have been illustrated recently by KOTEJA (1990).

The material used in the construction of these covers is secreted (i) by the well-developed wax gland systems typical of Coccoidea and also (ii) from other substances eliminated through the anus – *i.e.* the final products of metabolism. The range of integumentary glands which secrete the former are diverse and their secretions are transported to the body surface through specialized cuticular structures: pores, ducts, ductules and secretory setae (FOLDI, 1991). The shape taken by these secretions is dictated by both their chemical composition and by the shape of these cuticular structures, which act as moulding devices. These secretions are always mixtures, the two most common components being waxes and resins. The relative amounts of these components determine the characteristics of each secretion which, in turn, determine the color and hardness of the protective covers. These secretions also play an important role in the protection of the respiratory pathway and in assisting in honeydew elimination (FOLDI & PEARCE, 1985).

### Protective covers constructed from anal fluids

Based on the materials used in the construction of the test or cover, it is possible to distinguish five types of protective cover, namely those constructed from: anal fluids, mixtures of filamentous wax secretions and anal fluids, mixtures of filamentous and amorphous wax secretions, exclusively from amorphous wax secretions, and exclusively from filamentous wax secretions.

*Cyst formation.* Both sexes of species belonging to the subfamily Margarodinae have an unusual postembryonic development that includes an atypical second-stage nymph, commonly referred to as the cyst stage (Figs 8, 10, 12). The nymph of this cyst stage is legless and is completely enclosed in a shell constructed from anal fluids by the insect. The enclosed nymph has

FIGS 1-7. — **1**:. Adult female *Kermes roboris* Fourcroy (Kermesidae). **2**: Two adult female tests of *Unaspis yanonensis* (Kuwana) (Diaspididae). **3**: Group of adult female *Lecanodiaspis sardoa* Targioni-Tozzetti (Lecanodiaspididae). **4**: Adult female *Beesonia dipterocarpi* Green (Beesoniidae) located under the bark of its host plant. **5**: *Apiomorpha conica* (Frogatt) (Eriococcidae) showed the adult female in its gall. **6**: A colony of adult female *Gascardia madagascariensis* Targioni-Tozzetti (Coccidae). The scale insects are engulfed in a thick yellow test composed of secretions + excretions. **7**: Detail of Fig. 6 showing a fragment of test with the included females.
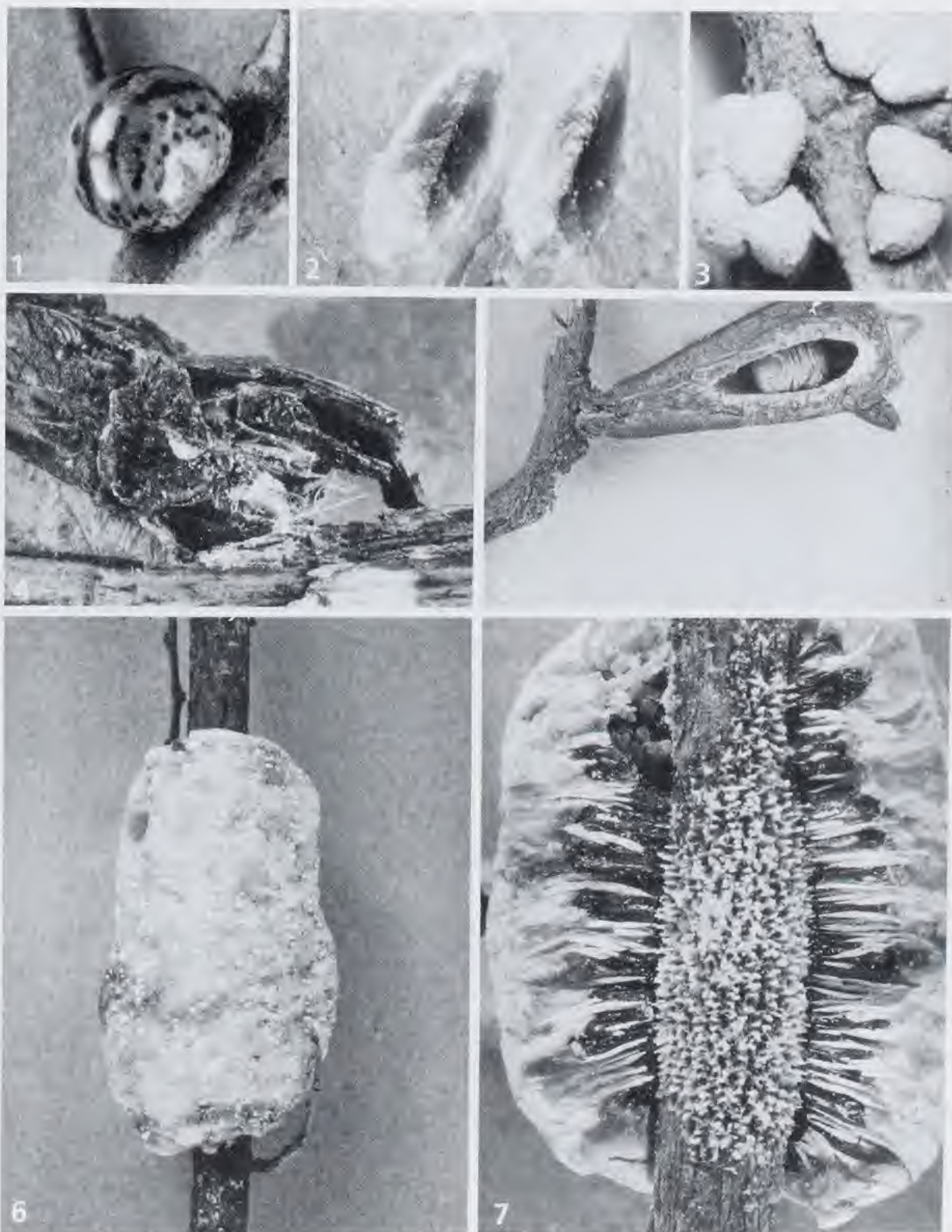
well-developed, functional mouthparts and, in most cases, the body is large and globular (although it may sometimes be elongate) but it always contains a large quantity of fat body. When the host plant lives in good environmental conditions (rain and sun assured), this cyst stage can last from several months to about a year, depending on the species. However, under unfavorable ecological conditions (*e.g.* prolonged dry period causing the death of the host plant), the cyst stage may be extended to several years. The second moult occurs within the cyst, giving rise to the adult female, which again possesses legs and antennae. Emergence of the adult female from the cyst is by first using the anterior legs to make a small opening in the shell wall and then squeezing through to exterior. This is possible due to the great flexibility of the body. In bisexual species, the adults then migrate to the soil surface to mate, and after this the females move back down into the soil and oviposit on or near the roots (FOLDI, 1990a).

The function of these cysts or shells has long remained unclear, mainly because the anatomy of the nymphs has not been well studied and because the structure and the processes of cyst formation have not been understood. The structure and formation of the cysts of *Margarodes formicarum, M. vitis, Eurhizococcus brasiliensis* and *Porphyrophora crithmi* were therefore studied, both experimentally and by the use of the scanning electron microscope (Figs 8-13). In most cases, the young first-instar nymphs settle on the host plant with their head down and their anus up. After settling and feeding, the secretion starts from the spiracular wax glands, while droplets appear from the anus and these slowly flow around the posterior end of the body and solidify (FOLDI, 1981). Sometimes several droplets are expelled in rapid succession. Even where the nymph settles in an oblique or horizontal position, the anal liquid flows over the body in the same way. The continuous feeding produces a rounded body and the anal liquid, which is regularly extruded, forms more and more overlapping layers on the body surface. If the anus is cauterized at this stage, the production of the anal liquid ceases and the construction of the shell stops. Alternatively, if the outer shell is removed experimentally, droplets continue to appear from the anus and shell formation commences once again, with the body gradually becoming covered with fine layers of secretion, the cyst finally becoming entirely enclosed. Electron microscope studies have confirmed the existence of 5 to 30 or more overlapping layers, each layer composed of an amorphous substance of equal or varying thickness, ranging from 5 to 100 μm thick (Figs 9, 11, 13). Thus, it appears that the structure of the cyst or shell is made exclusively from anal liquids eliminated by the nymph. The hardness, colour, size, shape and external surface morphology of these cysts varies considerably from one species to another. The hardness and colour are determined by the final metabolic products, and these are linked to the chemistry of the sap of the host plant and perhaps also to the secretions of some currently unknown glands located in the digestive system. In addition, the external surface of the cyst may include many extraneous particles, such as sand, earth or pieces of vegetation and these particles may completely mask the protective tests.

FIGS 8-13. — **8-9:** Cyst stage of *Margarodes formicarum* Guilding (Margarodidae). The cyst wall is formed by numerous overlapping layers of anal fluid. **10-11:** Cyst stage of *Margarodes vitis* (Philippi) (Margarodidae) with the detail of its wall structure. **12-13:** Cyst stage of *Porphyrophora polonica* Linnaeus (Margarodidae) and the detail of its wall showing the layered structure.

These cysts are generally located on the roots or collar of their host plants and are also referred to as "ground pearls". This name comes from their external appearance and their habitat. They are found in the sand or soil and are hard, round and pearl-like, often shiny and colorful, even sometimes slightly iridescent. There are ethnozoological reports of ground pearls being used for human utility. Like true pearls, ground pearls are strung on a filament and sold as necklaces in Bermuda and neighboring islands, in the Mediterranean area and wherever probably *Margarodes* pearls are found.

*Protective tunnel formation.* Anal fluids are also used by *Limacoccus* spp. (Beesoniidae) for the construction of their protective tunnel. In this genus, after the first moult, the second-instar females are located inside the exuviae. The produced anal fluid is pushed forward by the body's contraction and it is extruded through the exuvial split to the exterior. By the movement of the anterior part of the body, the nymph forms a semicircular tunnel in the anal substance which solidifies quickly. The nymph advances progressively in this tunnel and settles outside for the second moult. The wall of the tunnel is composed of numerous hard layers (FOLDI, 1995a).

*Structure and formation of separate tests using filamentous wax secretions and anal fluids.* The scale covers of the Diaspididae represent the most elaborate type of protective structure whose physical properties provide an effective barrier. They are formed from a combination of waxy filaments, mostly secreted by pygidial glands, which are cemented together by the successively extruded anal fluid, and formed either in a circular or an elongated shape by the movements of the body. The exuviae of previous instars are also incorporated into these covers (Fig. 2). Cover formation and how such factors as cauterization of the anus, delayed mating or insufficient food interfere with its construction are described in detail by FOLDI (1982, 1990b, 1990c). The cover formed by the Conchaspididae is constructed in a similar manner, except that it does not incorporate the exuviae and the anal secretions are not distributed actively over the dorsum (FOLDI, 1983).

*Structure and formation of separate tests using filamentous wax secretions and amorphous secretions.* Such species as *Cryptokermes brasiliensis* Hempel (Margarodidae), *Stigmacoccus asper* Hempel (Margarodidae) and *Ultracoelostoma assimile* (Maskell) (Margarodidae) form a protective test in which all stages of development are enclosed. The structure and the process of formation of the protective test was studied in *Cryptokermes brasiliensis* using SEM (Figs 14-21). The first-instar nymphs settled in crevices in the bark of *Vitis* sp. and started feeding. Waxy secretions were produced by multilocular wax glands which covered all the body; these were either short, curved secretions or long filaments (Fig. 14).

FIGS 14-21. — **14-15:** First-instar nymph of *Cryptokermes brasiliensis* Hempel (Margarodidae). The filamentous secretions covering the body is completed by a series of soft ball shaped secretions. **16:** Dorsal cicatrix of *Cryptokermes brasiliensis* Hempel (Margarodidae). **17:** Large spine-like structures with their amorphous secretions on the dorsum of *Cryptokermes brasiliensis* Hempel (Margarodidae). **18-19:** Detail of the coalesced ball shaped amorphous secretions among the filamentous secretion of *C. brasiliensis* Hempel (Margarodidae). **20-21:** Section of the cyst stage of *Cryptokermes brasiliensis* Hempel (Margarodidae) showing its wall structure.

Simultaneously, the perianal and anal wax glands started to produce a waxy anal tube which served to eliminate the honeydew. This tube reached twice the length of the 1st-instar body after only about 24h. Amongst this tangled, loose network of secretions some small, soft, ball-shaped amorphous secretions appeared which originated (i) from numerous cicatrices scattered on the dorsum and (ii) from large spine-like structures scattered between the cicatrices (Figs 15, 19).These amorphous secretions were scattered over the body and hardened slowly. They gradually increased in size and number so that they finally coalesced together. The shape of test covering the 1st-instar nymphs was fusiform, corresponding to the shape of the nymph's body, although the dimensions of the internal cavity was larger than the size of the body. After the first moult, the test (which was not completely finished yet) became more and more globular. The 2nd- and 3rd-instar nymphs continued to add new secreted material to the wall of the test, increasing its thickeness. By the time the insect was adult, the test was 5-6 mm in diameter and had a very rough external surface which was covered with bumps. In transverse section, the test wall was 0.5-0.6 mm thick and appeared to have an external layer formed from the ball-shaped amorphous secretions and an inner layer which was an amorphous mass (Figs 20-21). The test was very hard and the final colour was black. The adult females remained enclosed in this test and mating occurred through a small opening left by the anal tube of the immature stages; this aperture was also used by the newly hatched nymphs for dispersal. *Lecanodiaspis sardoa* Targioni-Tozzetti (Lecanodiaspididae) (Fig. 3) constructs a protective test which is formed from long filaments, secreted by the tubular duct wax glands, which are cemented together by amorphous secretions produced by the cribriform plates and the 8-shaped pores (FOLDI & LAMBDIN, 1995).

*Structure and formation of separate tests using exclusively amorphous secretions or mixture of amorphous secretions and anal fluid.* There are two types of amorphous secretions, the first is produced by the spine-like setae in Ortheziidae and the second by a variety of different wax gland systems found in the remaining scale insect taxa. In the majority of soft scales, the dorsal integument is covered by an amorphous and layered secretion, which increases the thickness of the dorsum and assists in its resistance to unfavorable external factors. In *Inglisia vitrea* Cockerell (and other Cardiococcinae), the cover is composed of a glassy, transparent covering composed of resin. This test is comparable to that found in the Asterolecaniidae, in which the test enclosing the female is also amorphous, hard and transparent. In *Cerococcus quercus* Comstock (Cerococcidae), the test of the adult females is an amorphous, yellow, smooth structure, although it has long waxy filaments on the inside. When the populations of these scales are dense, the tests fuse together to form a large mass on the twigs. The exuded mixture of amorphous secretions and anal fluid is so abundant in *Kerria lacca* (Tachardididae) and *Gascardia madagascariensis* (Coccidae) that it engulfs the entire colony forming the characteristic "stick secretions" on the twigs (Figs 6-7).

*Structure and formation of separate tests using exclusively filamentous secretions.* The use of only filamentous secretions for their protection is found on the adult females of many Margarodinae, Eriococcidae and on such soft scales as the Eriopeltinae or Filippiinae. The filamentous secretions forming either a loose network or a more structured test but it covers always some or all of the dorsal surface of the female.

*Ovisac-like structures.* After mating, the females of several groups (some Eriococcines, soft scales and Margarodids) produce filamentous secretions that enclose the female's body and also her eggs and newly-emerged nymphs. Other species construct a specific structure, the ovisac, which exclusively encloses the eggs and newly hatched nymphs. Thus, we can distinguish ovisac-like structures that enclose the female plus her eggs and nymphs from an ovisac constructed exclusively for protecting eggs and nymphs. The ovisac-like structure is found in female *Eriococcus buxi* (Fonscolombe), (Eriococcidae). This species construct a separate, felted sac-like test which encloses the body and eggs, except for a small hole at its posterior end. When observed by SEM, the wall of this test is made exclusively from a dense network of waxy filaments secreted by the tubular duct wax glands. Within this test, the eggs are covered by a loose network of short waxy filaments secreted by the ventral multilocular disc-pores. These protective tests cover the whole of the female's body and also the eggs and are composed of a loose network of filamentous waxy secretions. This ovisac-like structure cannot be considered as homologous to a true ovisac. For instance, mated female Margarodinae secrete by the multilocular wax glands distributed on the entire body a loose network of long waxy filaments, which encloses both the adult female and eggs. However, in addition, short curved filaments are secreted by the wax glands of the same type but with inclined loculi, that are distributed around the vulva, and these filaments cover the surface of the eggs. In some species, such as those in the genus *Gossyparia* (Eriococcidae), the filamentous secretions which protect the eggs only partially cover the adult female along the margins.

*Ovisac.* Many females Coccoids protect their eggs during embryonic development and then their newly hatched crawlers by constructing a true ovisac. Several unrelated groups of Coccoidea such as the iceryine Margarodids, Ortheziids, Pulvinarine soft scale, Kermesids – *e.g. Nidularia pulvinata* (Planchon) – and many mealybugs secrete a white ovisac. These ovisacs are characteristic structures, secreted by divers wax glands, which are clearly produced from beneath the posterior end of the abdomen of the adult females and are often ornate and have a characteristic shape. The presence of this type of ovisac in such a wide range of Coccoidea suggests that they evolved convergently. In groups with tubular duct wax glands, these are considered to secrete the external part of the ovisac, as in pulvinarine, filippiine and eriopeltine soft scales (HODGSON, 1994); indeed the Pulvinariini generally have three or four different types of ventral tubular ducts and also produce the most complex ovisacs within the Coccidae, in terms of the types of wax making up their ovisac (HODGSON, personal communication). In the simplest cases, the ovisacs are composed of two types of secretions: (i) an outer layer made of long filamentous waxy secretions which are thoroughly cemented together and which form a solid outer layer, and (ii) an inner layer composed of short, generally curved, waxy secretions which form a loose network around the eggs. In other taxa, such as in some soft scales species numerous types of wax glands may participate in its construction. An exception is found in the Ortheziids, in which the external part of the ovisac is made of (a) amorphous waxy secretions produced by the spine-like setae located in a large submarginal band on the abdomen and (b) by the long, thin filaments produced by the quadrilocular pores on the inner part. The construction of these ovisacs only starts after mating and is often finished whilst females are still laying. The best known example is the cosmopolitan *Icerya purchasi* Maskell which secretes an ovisac often

longer than its body, in which the hard, ornate and beautiful outer part is produced by two types of ventral wax glands: externally on the body margin are the large open centred pores and internal to these are the multilocular pores which form a broad submarginal band around the abdomen. The inner, looser part of the ovisac (which encloses the eggs) is secreted through the multilocular disc-pores around the vulva area. The red colour of the newly hatched 1st-instar nymphs, with black legs, are clearly visible within this white, cottony sac.

## BEHAVIORS WHICH HAVE EVOLVED TO EXPLOIT PROTECTION AFFORDED BY THE HOST PLANT

Many Coccoids settle in confined, protected feeding sites provided by their host plants, such under leaf-sheaths, leaf-axils, nodes of grass, in crevices or under bark, and on roots and root-crowns. This behavioral adaptation to protected feeding sites may be observed in most higher taxonomic groups in the Coccoidea, however the largest diversity is found in the Margarodidae *s.l.*

### Species which live beneath bark or in bark crevices

Species of the genera *Kuwania*, *Steingelia*, *Neosteingelia*, *Xylococcus* and *Xylococculus* live under the bark of such trees as *Pinus*, *Prunus* and *Quercus*. *Matsucoccus* spp. live in cracks and crevices or under the bark of *Pinus* spp. In these taxa, the cyst stage secretes a glassy test (as described above), while the adult females secrete white woolly waxen threads over the body.

*Species which oviposit beneath bark and otherwise live on the leaves. Stomacoccus platani* Ferris lays its eggs beneath the bark on the trunk of the host tree. The newly-hatched 1st-instar nymphs emigrate to the undersurface of the leaves. When fully grown, the mated females migrate back to the trunks and lay the eggs beneath the bark.

*Species which live beneath leaf-sheaths or on the nodes of grass stems.* Several eriococcine, pseudococcine and coccine species live under the leaf-sheaths or on the nodes of grass stems. Their bodies tend to be flattened dorso-ventrally and are only weakly covered by waxy secretions, although the body of *Aclerda berlesii* Buffa (which lives under the leaf-sheaths on the stems of *Arundo donax*) is surrounded by a large amount of glassy secretion. However, the body of *A. berlesii* is also flattened dorso-ventrally and becomes strongly sclerotized in old females.

*Gall formation.* Galls are products of host-insect interactions and are a response by the plant to chemical stimuli from salivary glands of the gall former. The gall-forming arthropod benefits in having an improved food supply, good environmental conditions and reasonable security. Extensive studies have been made on the gall-forming Coccoidea by GULLAN (1984a,b,c) and BEARDSLEY (1984). The majority of gall-forming scale insects belong to the Eriococcidae, which are abundant in Australia, principally on *Eucalyptus*. Galls formed by adult females of *Apiomorpha* Rübsaamen (Fig. 5) have species-specific morphology and vary greatly in size and shape, from cylindrical to globose and sometimes with arm-like extensions (GULLAN, 1984a,b). Galls of *Apiomorpha* are also sexually dimorphic, with the galls of males being much smaller than those of females. There are only two gall forming Margarodids currently known, *Matsucoccus gallicolus* Morrison and *Araucaricoccus queenslandicus* Brimblecombe. With *M.*

*gallicolus,* which is a pest on pitch pine, the feeding activity of the crawler causes the host-plant tissues to collapse, forming a depression beneath its body. By the time it moults to form the cyst stage, about six to nine weeks later, the host-plant tissue has grown to completely cover the Margarodid, except for a small hole. Once adult, the females generally disperse through this hole to the outside, although sometimes the hole is too small and the female is then obliged to stay and oviposit within the gall.

## ADAPTATIONS OF THE LIFE-CYCLE
## TO AVOID ADVERSE ENVIRONMENTAL CONDITIONS

The cyst of some species of *Margarodes* is highly resistant to adverse environmental conditions, which they are capable of surviving for a long time, only undergoing their last moult when conditions are again favourable. Prolonged absence of rain provokes the death of the host plant and, when again it rains, this water humidifies the soil around the cysts, which initiates their moult. MAYET (1896) noticed that the cysts of *Margarodes vitis* (Philippi) emerged as adult females once they had been immersed in water, even though they had been kept without food for seven years, while FERRIS (1919) reported an adult *M. vitis* emerging after seventeen years of storage. Like *M. vitis,* species which are capable of surviving such long periods have a highly resistant shell, with a thick and very hard wall. Similar observations were made by DE KLERK *et al.* (1980) on *Margarodes capensis* when females detached from their host plants under laboratory conditions could emerge during four successive years. My personal observations on the cysts of several *Margarodes* spp. is that their long-term survival is assured only for the nymphal stages and not for the adult females, even if the latter stay inside the cyst. The adult female of the cyst-forming species also have the ability to move from an unsuitable habitat to a suitable one, which is a characteristic that most scale insects have lost.

This protection afforded by the cysts is particularly important when the species are injurious to cultivated plants. For example, the cyst-forming Margarodids *(Eurhizococcus brasiliensis* and *Margarodes vitis),* injurious to vineyards in South America, are able to resist most control measures, including soil-applied insecticides (FOLDI & SORIA, 1989). This ability of the cyst-forming species to survive unfavorable conditions is almost certainly more widespread than we currently know but our observations are mostly limited to those species which are of economic importance.

## PROTECTION PROVIDED BY MODIFICATIONS OF THE BODY OF THE FEMALE

Alternative strategies for protection have been developed by some groups of Coccoids where the body of the adult female has become modified to provide protection, either by the ventral surface becoming invaginated to form a marsupium, as in several Margarodids, or by the dorsum become strongly sclerotized, as in Kermesids, many soft scales and Stictococcids.

### *Formation of a marsupium*

Although plesiomorphic in condition, the marsupium is the most remarkable invention for protecting the eggs and crawlers. Based on the method of formation of the marsupium, we can distinguish two types: (i) the internal marsupium is formed by a deep invagination of the integument within the body to form a large cavity, whereas (ii) the external marsupium is formed by depression of the ventral integument and the resulting cavity is covered by a secreted

operculum. An internal marsupium is found in a number of unrelated genera of Margarodids, *e.g.*, *Callipappus*, *Steatococcus* and *Etropera* spp. After mating, a deep invagination of the integument appears in the teneral female, either ventrally or in the posterior part of the abdomen, forming a cavity (MORRISON, 1928). Initially, the cavity is small but it progressively deepens during egg-laying. It is normally restricted to the abdomen but can extend even into the cephalothorax area. In species of *Steatococcus*, *Etropera* and *Perissopneumon*, the cavity is formed by the invagination of the sterno-abdominal integument. The vulva opens dorso-posteriorly into the marsupium and the eggs are laid directly into it. In *Callipappus* spp., this invagination is at the posterior end of the body, but can extend anteriorly within the body cavity as far as the head, as in *Callipappus westwoodi* Guérin-Méneville in which the long, narrow vagina opens antero-dorsally through the vulva into the marsupium.

The external opening of the marsupium in different taxa is highly variable. In *Steatococcus* spp., the opening is circular and is placed medially near the metathoracic legs, surrounded by numerous multilocular wax glands; in *Etropera* spp. (BHATTI & GULLAN, 1990), the opening is large, forming an arc, whose outer margins lie near the metathoracic legs but which lack wax glands, while in *Callipappus* spp. the opening is also large but is elongate and located at the posterior end of the body. In females possessing an external marsupium, a part of the ventral abdominal region containing the vulva becomes depressed and is then isolated from the exterior by an operculum composed of wax secreted by a large band of glands which surround the cavity. These glands produce large quantities of waxy filaments which become cemented together by an amorphous secretion. These opercula are solid, resistant to outside pressures and very hard to detach from the body. The eggs are laid inside this protective cavity and, once the nymphs have hatched, they leave through a small opening at the anterio-medial part of the operculum. There is considerable diversity in the size of these pseudo-marsupial pouches and their opercula. In species of *Aspidoproctus* and *Hemaspidoproctus*, the cavity is small, located in the central part of the abdomen and the operculum is thick and resistant. In *Gigantococcus maximus* (Newstead), the cavity is about 3 mm deep, incorporating most of the ventral surface of the abdomen, but with a rather softer and thinner operculum (BIELENIN, 1971).

*Using the dorsal surface of the body as the protective cover*

In this group, the dorsal cuticle of the female becomes thickened and strongly sclerotized at maturity, whereas the ventral surface remains thin and often becomes deeply invaginated, forming a cavity under the body which becomes a brood chamber used for holding the eggs and the crawlers. This method of protection is typical of the Kermesids, many soft scales – *e.g.* species of *Saissetia*, *Coccus*, *Parthenolecanium* and many others (HODGSON, 1994) – and the Stictococcids (Fig. 1). However, other soft scales secrete a thick waxy cover (*e.g. Ceroplastes* spp.) but, despite this, the dorsum becomes heavily sclerotized at maturity and the venter deeply invaginated, forming the brood chamber. The eggs and crawlers are protected also under the body of *Auloicerya acaciae* Morrison & Morrison (Margarodidae) (GULLAN, 1986). LOWER (1957) reported an interesting example in the Pseudococcidae. Species of *Epicoccus*, which live in arid conditions in Australia, develop a thickened and chemically modified dorsal integument, which is considerably expanded in comparison to the venter, thus offering excellent protection of the female and her progeny against the drying winds, high temperature and low relative humidity of their environment.

*Protection by ants*

Facultative mutualistic relationships exist between several groups of scale insects and ants. This relationship is of reciprocal benefit because for the ants the sugar-rich honeydew represents a food supply, and for the Coccoids the ants provide some protection against natural enemies, *i.e.* predators and parasitoids. Furthermore, ants by removing honeydew, reduce contamination of the Coccoids and so stop fungus development, which is injurious to the host plant and the scale insects. Further protection may provided by ants that construct protective covers over Coccoid aggregations (FOLDI, 1984). Recently, WILLIAMS (1978) and HODGSON (1994) have described some deep morphological modifications, *e.g.* spiracular and anal adaptations, characterizing scale insects living an intimate relationships with the ants in their nests.

## PHYLOGENY

Currently, cladistic phylogenetic hypotheses for the entire Coccoidea are lacking, since only keys and classification are available to show the relationships of the higher taxa within the Coccoidea. This cladistic analysis presents one of the first attempts to produce a preliminary estimate of the Coccoid phylogeny. The genera used are representatives of the traditionally recognized families, however these families may not necessarily be monophyletic.

*Character and character state definitions*

*Adult female.*
1. Locular pores: (0) absent; (1) present
2. Wings: (0) present; (1) absent
3. Dorsal tagmosis: (0) distinct; (1) indistinct
4. Cornicles: (0) present; (1) absent
5. Abdominal spiracles: (0) present; (1) absent
6. Ostioles: (0) absent; (1) present
7. Cicatrix-like structures: (0) present (1) absent
8. Legs: (0) well developed; (1) reduced or absent
9. Eight-shaped tubular ducts: (0) absent; (1) present
10. Tubular ducts: (0) absent; (1) not invaginated; (2) invaginated
11. Microtubular ducts: (0) absent; (1) present
12. Pores with thoracic spiracles: (0) absent; (1) present
13. Spiracular pore rows: (0) absent; (1) simple row; (2) double rows
14. Location of anus: (0) postero-dorsum or posterior; (1) middle dorsum or venter
15. Translucent pores on hind legs: (0) absent; (1) present
16. Dermal papillae near spiracles: (0) absent; (1) present
17. Anal plates: (0) absent; (1) simple; (2) double
18. Anal opening: (0) simple opening; (1) anal ring; (2) anal ring with setae and pores; (3) anal ring with setae
19. Mouthparts: (0) present; (1) absent
20. Number of instars: (0) 5 instars; (1) 4 instars; (2) 3 instars
21. Tarsal segments: (0) 2 segments; (1) 1 segment

*First instar.*
22. Antennal segments: (0) 6 segments; (1) 7; (2) 5 - 3

23. Apical antennae setae: (0) few hair-like setae; (1) seate with a single spine; (2) hair-like setae with stout setae; (3) numerous hair-like setae (4) hair-like setae with fleshy seta or setae
24. Pores with thoracic spiracles: (0) absent; (1) on meso + metathoracic; (2) only mesoth.
25. Astero-type 8-shaped pores: (0) absent; (1) present
26. Bilocular pores: (0) absent; (1) present
27. Trilocular pores: (0) absent; (1) present
28. Simple pores: (0) absent; (1) present
29. Tarsal campaniform pore: (0) present; (1) absent
30. Tarsal digitules: (0) absent; (1) present
31. Number of claws: (0) 2 claws; (1) 1 claw
32. Claw digitules: (0) absent; (1) present seta-like; (2) knobbed
33. Denticle on claw: (0) absent; (1) present
34. Tibia and tarsus length: (0) ti > ta; (1) ti = ta; (2) ta > ti
35. Enlarged setae: (0) absent; (1) present
36. Femoral setae of hind legs: (0) several ; (1) 1 seta or absent
37. Tibial setae of hind legs: (0) several ; (1) 1 seta or absent
38. Tarsal setae of hind legs: (0) several ; (1) 1 seta or absent
39. Setae on legs: (0) abundant on all segment; (1) frequent; (2) few
40. Long caudal setae: (0) absent; (1) present
41. 8-shaped tubular ducts on the head: (0) absent; (1) present
42. Labial segments: (0) 4 segments; (1) 3 segments; (2) 1 or 2
43. Labial setae: (0) 12 or more; (1) 7 - 11; (2) 6 or less
44. Quadrilocular pores: (0) absent; (1) present
45. Quinquelocular pores: (0) absent; (1) present

*Adult male*
46. Compound eyes: (0) present; (1) absent
47. Number of simple eyes: (0) absent; (1) 16; (2) 14; (3) 10; (4) 4
48. Antennal segments: (0) < 9 segments; (1) 9 segments; (2) 10 segments
49. Abdominal spiracles: (0) present; (1) absent
50. Hindwings: (0) present; (1) present as hamulohalteres; (2) absent
51. Hamulohaltere setae: (0) absent; (1) 3-4; (2) 2;
52. Lateral view of aedeagus: (0) curved; (1) straight
53. Postocular ridge: (0) dorsally weak or absent; (1) dorsally well present
54. Dorsal pore clusters on abdomen: (0) absent; (1) one median on VI and VII; (2) one median on VIII; (3) two separated clusters on VIII.

Analysis of the character data in Table 1 with the heuristic search algorithm of Paup resulted in two equally parsimonious cladograms. The strict consensus tree in Figs 22-23 (Tree length: 190, Consistency index (CI): 0.40, Retention index (RI): 0.59) shows some unresolved relationships among the genera. The two trees differed in the placement of Coccus, which either was placed with the pit scales (*Astero-Cero-Lecanodiaspididae*) or was part of the group of relationships among the genera. The two trees differed in the placement of Coccus, which either *Aclerda + Tachardia*. The placement of *Micrococcus* is also problematic since it is the sister group to the *Stictococcus*+. According to MILLER & WILLIAMS (1995), the Micrococcidae is most closely related to the Aclerdidae. *Stigmacoccus* (Margarodidae *sensu* MORRISON, 1928) is the sister group of all other scale insects and is characterized by two following autapomorphies: anal ring (18.1) and two hamulohalteres setae (51.2). *Matsucoccus* + *Margarodes* (Margarodidae *s.l.*) are characterized by the following synapomorphies of the 1st instar nymph:

TABLE 1. — Character matrix used for the cladistic analysis of the Coccoidea.

```
                    1111111111222222222233333333333444444444455555
                    12345678901234567890123456789012345678901234
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|  |  |
|---|---|
| *Eriosoma* | 000000000000000000000000000000000000000000000000000000 |
| *Myzus* | 000000100000000000000000000000000000000000000000000000 |
| *Stigmacoccus* | 11110000000000000102000000000011020000000020000000012003 |
| *Carayonema* | 11110000000000000302121000000011020000000020000??????????? |
| *Matsucoccus* | 11110000000000000012000000000010120201102102200002011012 |
| *Margarodes* | 11110010000000000012122000000101002010021022000?????????? |
| *Orthezia* | 11110010000000000301101000000111111000100101000101 1013 |
| *Phenacoleachia* | 11111110000000000030111300000011211100000000001120100 13 |
| *Conchaspis* | 11111010000000000002100000001112170111210110014011 0010 |
| *Planococcus* | 1111111001000010030110300010111202000011010001421100 03 |
| *Eriococcus* | 1111101002110010030210300010111212100011010011411100 13 |
| *Kermes* | 11111011020000000102?040010001121211002101001132110013 |
| *Dactylopius* | 1111101002000000002021020000011120210002001001142127013 |
| *Asterodiaspis* | 11111011010110000202?041101101110200102102100142127010 |
| *Cerococcus* | 11111011020120000302?021100101121200002101001142120010 |
| *Lecanodiaspis* | 11111011020110000302?011101101121200002102101142112110 |
| *Stictococcus* | 11111010011111000202124000000112000000210200014012?113 |
| *Coccus* | 11111010020110002302104100111112110000210221114212?110 |
| *Micrococcus* | 11111010020100002301124101011112000000110200010012?0?0 |
| *Aclerda* | 11111011010100001201?031000111121010002102101142127000 |
| *Tachardia* | 11111011020100001302?032000011121001002102201142127110 |
| *Phoenicoccus* | 11111011110101010202?0410000011211011121120011401270?0 |
| *Halimococcus* | 11111011110000010102?0120000011200011121122001401270?0 |
| *Beesonia* | 11111011110100000101?231000011121201112112110140110170 |
| *Chionaspis* | 11111011110100000002?242001001120201112112200142110110 |

tarsal campaniform pore (29.1); femoral setae on hind legs (36.1); setae on legs (39.1); long caudal setae (40.1) and absence of the mouthparts in adult females (19.1). However, the family Margarodidae appears to be paraphyletic because of the position of *Stigmacoccus* on the tree and the Margarodidae should be restructured into monophyletic groups. A cladistic analysis of the Margarodidae *s.l.* and related groups is currently undertaken by the author (FOLDI, unpublished). In the remainder of the tree, the monophyletic family Carayonemidae is the sister group of the other Coccoidea and it is characterized by one autapomorphy, apical antennae with a single spine (22.1).

The autapomorphies representing cladistic diagnoses of the scale insects genera are as follows: *Orthezia*: setae frequent on legs (39.1); presence of quadrilocular pores (44.1); 9 antennal segments (48.1) and presence of 3-4 hamulohalter setae (51.1). *Phenacoleachia*: Ostioles present (6.1); 6 antennal segments (22.0), reversal and, labial segments (42.0), reversal. *Conchaspis*: femoral seta1 on hind legs (36.1); tibial seta on hind legs (37.1); tarsal seta on hind
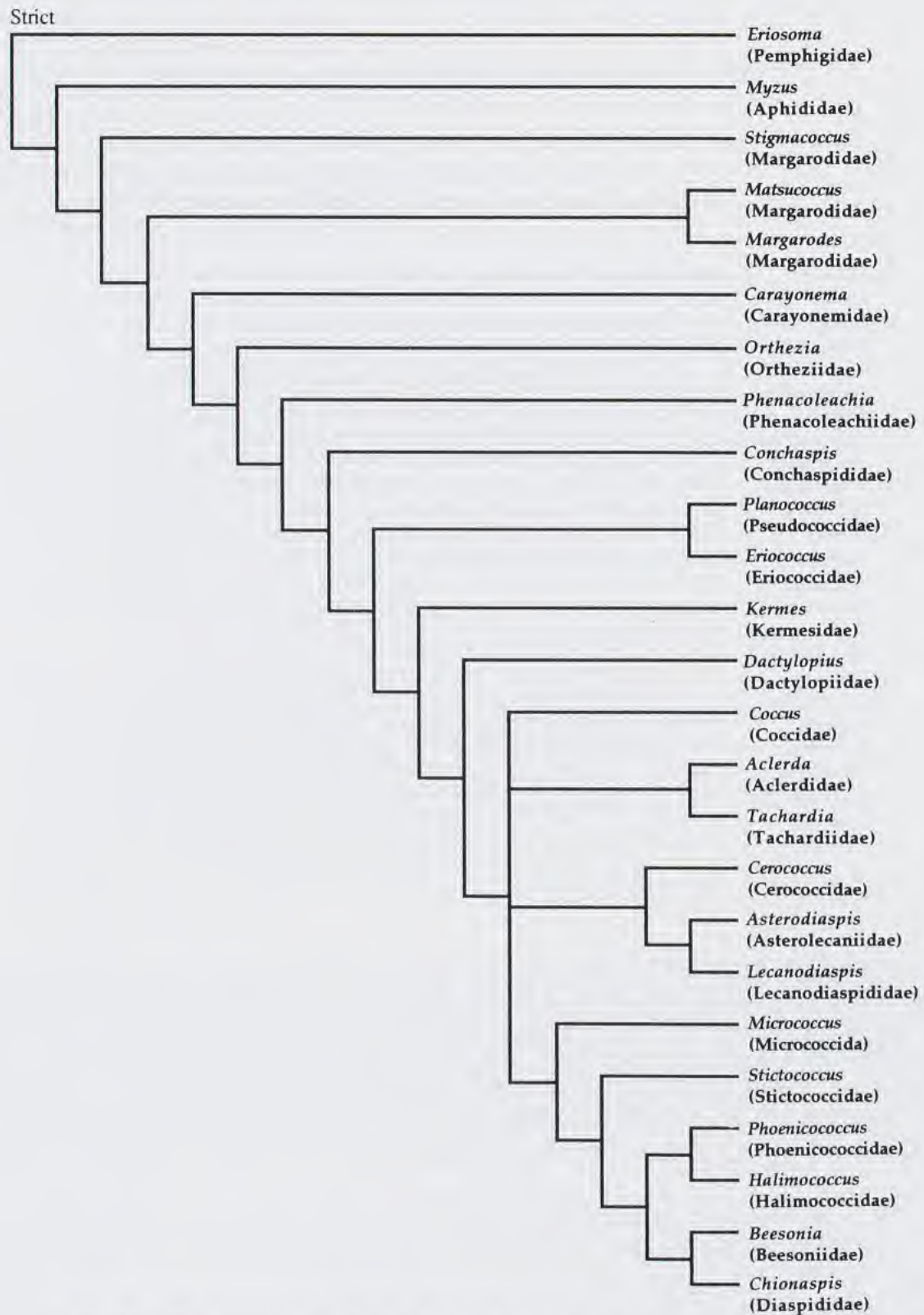
Strict

*Eriosoma*
(Pemphigidae)

*Myzus*
(Aphididae)

*Stigmacoccus*
(Margarodidae)

*Matsucoccus*
(Margarodidae)

*Margarodes*
(Margarodidae)

*Carayonema*
(Carayonemidae)

*Orthezia*
(Ortheziidae)

*Phenacoleachia*
(Phenacoleachiidae)

*Conchaspis*
(Conchaspididae)

*Planococcus*
(Pseudococcidae)

*Eriococcus*
(Eriococcidae)

*Kermes*
(Kermesidae)

*Dactylopius*
(Dactylopiidae)

*Coccus*
(Coccidae)

*Aclerda*
(Aclerdidae)

*Tachardia*
(Tachardiidae)

*Cerococcus*
(Cerococcidae)

*Asterodiaspis*
(Asterolecaniidae)

*Lecanodiaspis*
(Lecanodiaspididae)

*Micrococcus*
(Micrococcida)

*Stictococcus*
(Stictococcidae)

*Phoenicococcus*
(Phoenicococcidae)

*Halimococcus*
(Halimococcidae)

*Beesonia*
(Beesoniidae)

*Chionaspis*
(Diaspididae)

FIG. 22. — Strict consensus tree showing the hypothetical relationships within the Coccoidea.

FIG. 23. — Strict consensus tree with the character numbers.

legs (38.1); labial setae (43.1). *Planococcus* and *Eriococcus* group is characterized by the following synapomorphies: presence of translucent pores on hind legs (15.1); trilocular pores present (27.1); setae on legs frequent (39.2). *Kermes*: presence of anal ring (18.1); legs (8.1); femoral setae on hind legs (36.1) and the number of simple eyes (47.3). *Dactylopius*: anal ring with setae and pores (18.2) and apical antennae setae (23.2). The *Cerococcus* + *Asterodiaspis* + *Lecanodiaspis* group is supported by one apomorphy, the presence of the Astero-type 8-shaped pores. The *Coccus* + *Aclerda* + *Tachardia* are characterized by two synapomorphies: anal plates 17.1 and 2) and labial setae (43.1 and 2). *Micrococcus*: number of instars (20.1); bilocular pores (26.1) and setae on legs (39.1). *Stictococcus*: presence of microtubular ducts (11.1); presence of spiracular pore row (13.1); location of anus on the middle dorsum or venter (14.1) and two separated dorsal pore clusters on VIII (54.3). *Phoenicococcus* + *Halimococcus* are supported by one synapomorphy: dermal papillae near spiracles (16.1). *Beesonia* + *Chionaspis* are characterized by two synapomorphies: tarsus longer than tibia (34.2) and the hamulohaltere are presents (50.1).

Some nodes are supported by a few characters, such as the node relating *Planococcus* + *Eriococcus* to *Kermes*+ is supported by one character, however there is a strong apomorphy, namely the presence of tubular ducts (10.1-2). The node relating the *Coccus* to Aclerda+ is also supported by a strong apomorphy, the absence of the hamulohalteres (50.2). In contrast, some other nodes are well supported, for example the *Orthezia* to *Phenacoleachia*+ is supported by

five characters: absence of cicatrix-like structure (7.1); presence of tarsal digitules (30.1); presence of denticle on claw (33.1); presence of enlarged setae (35.1) and the labium with 3 segments (42.1). The node relating *Phoenicococcus* to *Halimococcus*+ is supported by seven characters: legs are reduced or absent (8.1); eight-shaped tubular ducts (9.1); femoral setae on hind legs (36.1); tibial setae on hind legs (37.1); tarsal setae on hind legs (38.1); eight-shaped tubular ducts on the head (41.1) and labial setae (43.1-2).

The cladistic analysis shows the scale insects are a natural group. The monophyly of the Coccoidea is supported by the following four autapomorphies of adult females and nymphs: the presence of locular pores (1.1), the absence of wings (2.1) the occurrence of indistinct dorsal body tagmosis (3.1) and the presence of a single clow on the legs (31.1). However, the relationships of several family-group taxa, as well as the monophyly of some families remain controversial and not well established. Further studies will be needed, with more taxa and particularly more anatomical or morphological characters, before the relationships are well understood.

## EVOLUTIONARY SCENARIOS

Two major attributes being studied here (habitats and protective structures) were then mapped onto the cladogram. From this it was possible to propose an hypothesis of the ancestral states and then their evolution during the subsequent diversification of the superfamily. Since the scale insects are sedentary (a few groups are weakly mobile), the term habitat here refers to the final settling and feeding site on the host plant. There are difficulties in deriving evolutionary scenarios to explain the evolution of the habitats and protective structures for the entire family-level taxa of Coccoidea. In large groups, such as the Margarodidae, Diaspididae, Coccidae and Pseudococcidae, position on the plant is highly variable in many lower taxonomic groups and, similarly, many taxa within a family have quite different types of protection. For example, the Margarodidae *s.l.* constitutes a large heterogeneous group with considerable behavioral diversity, so that we can find scale insects in galls, on roots, on or under bark, or on twigs or leaves, depending on genus or species or even instar. For these reasons, it is suggested that future research on the evolutionary scenarios of scale insects should concentrate on diversification within families.

For the "habitat evolution" five attribute-states were used: 1. bark; 2. branches; 3. roots; 4. leaves; 5. stem of grasses. In the most parsimonious optimization, the cladogram (Fig. 24) shows that the ancestral habitat attribute (feeding site) is equivocal and currently we can not choose between the aerial (bark) or underground (roots) habitats. However, the bark or roots appears the most probable ancestral state since it requires only 8 changes against 9 for branches. This scenario of other habitats being subsequent derivations implies 10 changes for leaves and stem of grasses. *Stigmacoccus* lives on the bark of *Inga* spp. *Matsucoccus*, is restricted exclusively to the bark and branches of *Pinus* spp. Root feeding (*Margarodes*) has been adopted on a large diversity of plants, and is particularly characteristic of the cyst-forming Margarodinae. This unique life-style may have evolved from that of leaf litter-inhabiting species which gradually moved underground and undoubtedly represents a secondary adaptation. *Carayonema* is close to the supposed ancestral state, living on the superficial roots and having well developed legs, in contrast to *Margarodes* which live on deeper underground roots and have highly modified first
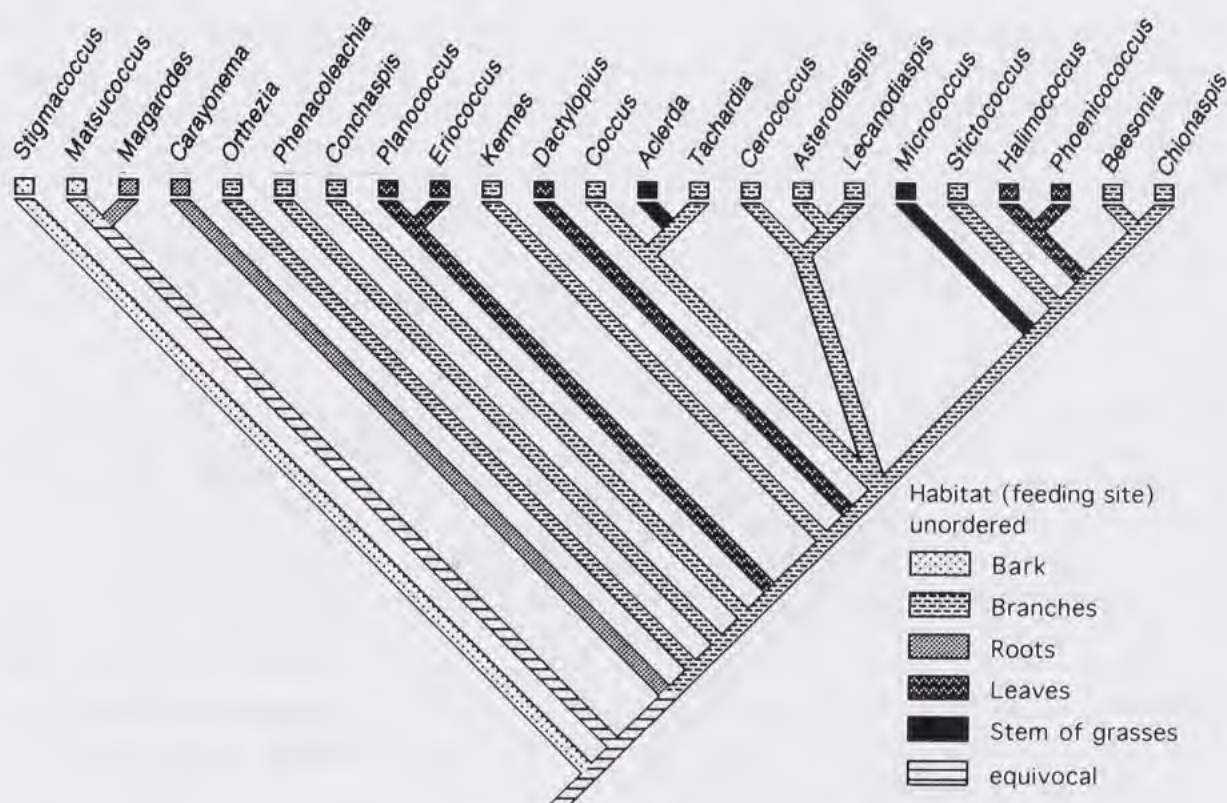
FIG. 24. — Hypothetical evolution of the feeding site (habitat) in the Coccoidea, based on the phylogenetic tree in Fig. 22.

legs which are enlarged as digging organs. The leaves habitat has arisen twice independently in *Phoenicococcus + Halimococcus* and *Planococcus + Eriococcus + Dactylopius*. An importantchange has arisen in the clades of *Micrococcus* and *Aclerda* with a shift from woody hosts to grass host plants. Such a shift, however, was not particularly successful as no wide adaptive radiation can be observed in these clades. The branches habitat represents the most exploited feeding site among the Coccoidea, especially by the most speciose groups such as the Coccidae and Diaspididae.

For "protective structures", six states, according to the material used for protection, were identified: 1. filamentous secretions, 2. amorphous secretions, 3. cyst (anal fluid), 4. test (formed by one or two types of secretions *e.g.* amorphous or filamentous secretion or both). 5. composed test (formed by filamentous secretions and anal fluid). 6. associated test (formed by filamentous secretions + anal fluid + exuvium) (Fig. 25). The type of protection is strongly associated with habitat and a change in the protective method is correlated with a major change in way of life. Thus, the adaptation of Margarodinae for underground life is accompanied by the use of anal fluid in the nymphal instars, whereas Margarodid species adapted to live under bark during the nymphal instars secrete amorphous substances. In both cases, the adult females are mobile while
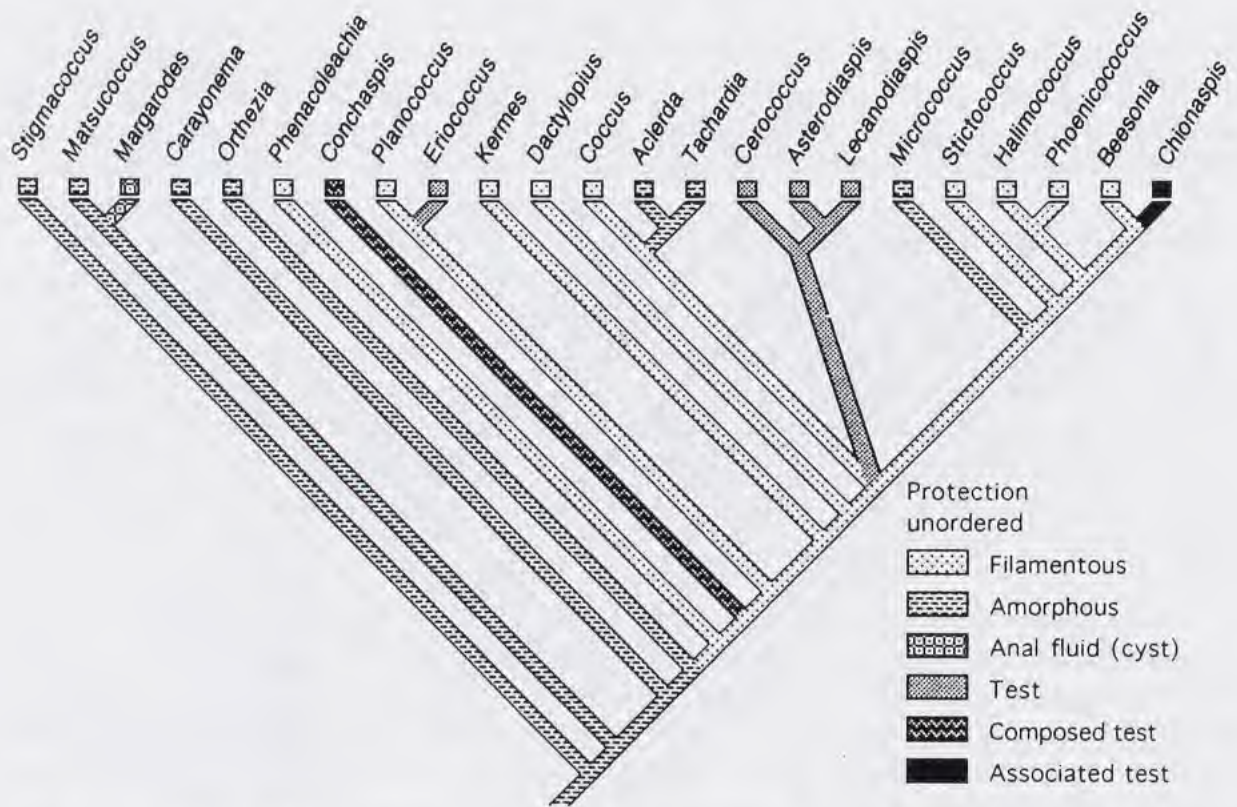
FIG. 25. — Hypothetical evolution of the protective structures in the Coccoidea, based on the phylogenetic tree in FIG. 22.

searching for males, but after mating produce filamentous secretions. In cases for which the material used for protection varies in different stages of development, then the attribute state considered was that of the nymphal stage. The most parsimonious scenario for the protective structures suggests that the ancestor was protected by amorphous secretions since it requires only 8 changes against 9 for filamentous secretions. In *Stigmacoccus*, *Matsucoccus* and *Carayonema* spp., these amorphous secretions are secreted by cicatrice-like structures, while in the Ortheziidae, in which they evolved independently, they are secreted by the spine-like setae. This scenario implies 10 changes for anal fluid and for various tests. It is interesting to note that the use of anal fluids for constructing protective structures is found both in the basal clade Margarodidae then Conchaspididae and in the Diaspididae. In general, for the group constituting mainly the lecanoid and diaspidoid taxa, it appears that the filamentous secretions were the ancestral state, with three separate lines evolving from it: a felted sac (Eriococcidae), secreted tests (Lecanodiaspididae) and the composed test (Conchaspididae, Diaspididae). Under phylogenetic inference, this scenario for the evolution of protection suggests that lineage diversification was achieved with 9 changes within the superfamily. This number obviously is related to the size of the data set. Filamentous secretions represent the material most commonly used for protection. These secretions have evolved independently in all clades of Coccoidea and are involved not only in protecting the body but also are vital to the functions of the respiratory, reproductive and excretory systems.

The validity of these proposed evolutionary scenarios depends on several factors: firstly, the validity of the proposed phylogeny, which was developed using heuristic methods and, therefore, is clearly approximate; secondly, the assumption that the families studied are monophyletic, which should be controlled in a more detailed cladistic analysis, and thirdly, the acceptance of the selected genera represent the characteristic of the families. GULLAN (personal communication) would add further factors like the robustness of the data matrix, as the addition of further characters or taxa may alter tree topology; and the subjective nature of scoring of the character states (homologies may not be correctly recognized). Of course, the corroboration or refutation of these results is dependent on further testing with new data.

## DISCUSSION

One of the major evolutionary events in scale insect history led to adult females being neotenic and wingless, thus causing them to take on a sessile trophic habit, exploiting various microhabitats on the host plants while sucking sap from their host's vascular tissues. This sedentary habit ensures that scale insects have a continuous, reliable food supply for minimal energy expenditure but with a major disadvantage that it can only be successful if the host-plant remains healthy. In addition, being sessile makes them vulnerable to adverse environmental conditions and attack by natural enemies, so they have evolved a range of strategies to improve their chances of survival and reproductive success. The manner of protection may vary as a function of the developmental stage, as in most species living in protected habitats, or may be constant throughout development, as in most species living in aerial habitats.

It is obvious that optimal defensive strategies are those which give the greatest reduction in mortality and the greatest increase in reproductive success with the least energetic cost. One of the most widespread of these defense strategies is the use of a series of wax secretions produced by an extensively developed wax gland system, even though this involves a considerable energy investment. Obviously, the resources directed to secretions could not be allocated to oocyte production for the direct enhancement reproductive success. The use of anal fluids represented progress in the energetic dispensation of resources because their use is particularly economic. Indeed, using their own excreta, these insects would appear to invest very little energy in the production of the protective covers (cysts, composed tests, associated tests) compared with those which secrete wax from dermal wax glands to manufacture their protective covers. Another ingenious method of protection for the scale insects, characterizing numerous unrelated taxa, consisted of behavioral adaptations that allow exploitation of the protection offered by the host plant (such as cryptic life beneath the bark, under leafsheaths or nodes of grass stem or gall formation), which lead to the reduction of the wax gland system. The exploited host plant affords protection requiring less energy expenditure. The cyst-forming Margarodinae found an alternative strategy to escape adverse environmental conditions by changing their generation time, as exemplified by the well known *Margarodes vitis* which can remain dormant but alive for up to seventeen years. Apparently, simplest protection evolved in several unrelated groups by the modification of the female's own body (*e.g.* the marsupium of some Margarodids or the strongly sclerotized dorsum of many soft scales, Kermesids or Stictococcids) which functions in the same way as a secreted protective cover.

What are the most successful scale insects and what is their defensive strategy ? These are the Diaspidids – small legless insects – which mostly live on the branches and leaves. They

construct, with an energetic compromise (*e.g.* using a mixture of secretions and anal fluids), the most elaborate test among the Coccoidea, which is formed throughout their life cycle, serving to protect the insect from the time of the 1st-instar nymph through to the ovipositing adult. The efficiency of this protective cover is reflected by the success of the group since it includes more than 2000 species distributed worldwide. In the case of the soft scales (the Coccidae), which have nearly 2000 species and tend towards a large body size, a series of alternative strategies has evolved, some using various and (sometimes considerable) secreted substances, others using plant or body protection. The mealybugs, also have nearly 2000 species, are weakly mobile, and produce various waxy secretions (but these are much less important than those in the soft scales) and also occasionally use plant protection. In the Margarodidae, species such as those in the genus *Matsucoccus* (Margarodidae *s.l.*) appear to represent the earliest known scale insects (fossils) but, at the same time, appear similar to the *Matsucoccus* spp. of today, it is likely they were protected in a similar manner, *e.g.* by secreted amorphous and filamentous secretions.

Most successful groups are adapted to the aerial part of woody host plants, particularly on the branches, which are the most exploited feeding sites by Coccoidea and associated with divers system of defense. The protection in relation with this habitat (branches) shows an evolution from simple to complex structures: branches + amorphous secretions; branches + filamentous secretions; branches + test; branches + composed test and branches + associated test. The filamentous secretions, principally extruded by the pores and ducts, represent the material most utilized for protection. Each taxon has found its own solution in ensuring their evolutionary success. It may be significant that the groups which exhibit different types of protection during their life-cycle are characterized by a low species richness.

There appears to be an obvious coadaptation between body size, habitat selection and defense and this has caused convergent evolution of protection strategies dictated by habitat-required defense strategies. A trend is observed in the defense strategies of scale insects to find a compromise between energy usage and the efficiency of the protective structures. Understanding of the extant habitats and protection and how they could have evolved in scale insect history necessitates observation of their early evolution. Based on paleontological data, the earliest known scale insects belong to the Margarodid genus *Matsucoccus*, from the Lower Cretaceous, living on *Pinus* spp., and the fossil Coccoids from Tertiary amber, within which all the main lineages of current families within Coccoidea have been found, are mainly Margarodids. According to SHCHERBAKOV (1990), ancestors of scale insects were aphid-like four winged Precoccids but the current evolutionary hypotheses regarding the early evolution of Coccoids suggests that they lived in leaf litter. WIGGLESWORTH (1972), in his book "The life of insects" suggested that the insects may have evolved in the litter layer. KOTEJA (1984, 1985, 1990a,b) has also postulated that Coccoids may have evolved in the forest litter probably during the Permian to Jurassic, where they acquired adaptations to either an epigeic (all main lineages of Coccoidea) or an hypogeic (Margarodinae) life behavior. This adaptive radiation of early Coccoids may have allowed them to colonize most parts of their host plants and it is a reasonable assumption that they displayed, at this period, most of their present morphological characteristics. This is what we observe with the Margarodidae *s.l.* They exploit more feeding sites (roots (Margarodinae), bark and branches (Matsucoccinae, Steingeliinae), under bark (Xylococcinae), leaves (*Stomacoccus platani*) and galls (*Araucaricoccus* spp., *Matsucoccus gallicus)* than the Necoccoids, which are more specialized. A probable secondary radiation started in the

Cretaceous, with the colonization of the gymnosperms and angiosperms, mainly involving the recent Coccoids. Most of the Neococcid fossils that originate from the upper Cretaceous are similar to contemporary forms which have evolved independently in various directions, colonizing all parts of their host plants. KOTEJA (1985) suggested also since primary habitat was leaf litter, the scale insects may have fed on the dead and decaying remains of plants, particularly on fungi and bacteria that are responsible for plant decay. Although the mouthparts of scale insects are adapted for piercing and sucking nutritious fluids from plants, it is possible to admit that they have could used decayed material as food in their early evolution. Recently, *Carayonema orousseti* (Carayonemidae), was collected in the leaf litter in South America but actually it fed on roots located near the soil surface (J. OROUSSET, personal communication). Another Coccoid, *Laurencella marikana* (Margarodidae) was found in a similar situation. A colony of these Margarodids had settled on the parts of the roots located at the soil surface, covered by the leaf litter and stones (FOLDI, 1995b). We can suppose that similar situation may have occurred in the early evolution of Coccoids, where some aerial part of the roots were available for a transit to a new feeding site or habitat.

To provide a fuller explanation for the adaptive evolution (habitat and protection) of scale insects, we need to carry out a detailed phylogenetic analysis on the Margarodidae *s.l.* since several fossils show that some of them had already reached their extant morphological organization early in Coccoid evolution.

## ACKNOWLEDGEMENTS

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